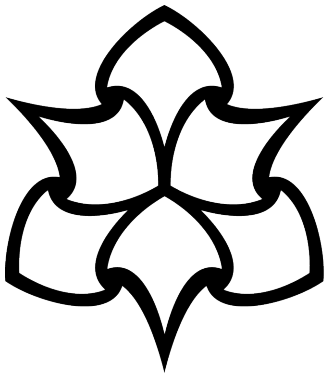

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Contributions in honour of Theo C.M. Bakker: *Testing, not guessing*

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In July 2017, Theo C.M. Bakker officially retired as a Professor in Animal Ecology at the University of Bonn, Germany. This occasion was celebrated with a symposium hosted by Thomas Bartolomaeus, Director of the Institute for Evolutionary Biology and Ecology, and organized by Timo Thünken and Ingolf Rick. At this event, former colleagues and students gave insights into their recent research. This special issue of *Evolutionary Ecology Research* is a companion to this symposium, including contributions of Theo's current and former group members as well as of colleagues from Bonn and abroad. The contributions to the symposium and to the special issue cover a broad variety of topics, including sexual selection (a talk by Manfred Milinski), social evolution [a talk by Joachim Frommen; paper by Josi *et al.* (2018)], applied ecology and conservation [talks by Sarah Kraak and Dominique Mazzi; paper by Hilgers *et al.* (2018)], host–parasite interactions (Thünken *et al.*, 2018), phenotypic plasticity (Meuthen *et al.*, 2018b; Schmoll *et al.*, 2018), population genetics (Müller *et al.*, 2018), and animal cognition and behavioural physiology (Mehlis-Rick *et al.*, 2018; Pannhausen *et al.*, 2018; Schluessel and Ober, 2018). They therefore reflect Theo's broad scientific approach and his multifaceted interests in the field of animal ecology.

Indeed, Theo's master's thesis, which he conducted at the University of Groningen in The Netherlands, consisted of three different projects covering theoretical ecology, population genetics, and behavioural genetics. Theo's first paper (van Oortmerssen and Bakker, 1981) emerged from the behavioural genetics part. Using selection lines, he demonstrated that aggressiveness in house mice (*Mus musculus*) has a heritable component. For his subsequent PhD studies, Theo moved to the University of Leiden, which was a hotspot in the emerging field of ethology at that time. In Leiden, Theo was supervised by Piet Sevenster, a former assistant of Niko Tinbergen. Consequently, Theo was a second-generation student of Tinbergen, a fact he has always been proud of (Bakker, 2010) and which is conveyed in his strict and fine-tuned experimental approach when studying animal behaviour. In Bakker (2010), Theo provides an overview of Tinbergen's research and his impact on the Dutch ethologists while looking back at his time in Leiden from a very personal point of view.

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In Leiden, Theo continued to follow his interest in the genetics of behaviour, working on a study organism that would become his main model species throughout his subsequent career: the threespine stickleback (*Gasterosteus aculeatus*). This small fish shows pronounced sexual dichromatism, with males being famous for their conspicuous nuptial coloration (i.e. red throat and blue eyes; see Fig. 1), extended paternal brood care, and a latent willingness to engage in aggressive interactions with its neighbours (Wootton, 1976). The threespine stickleback is easy to keep and breed in the lab, making this species a perfect model system for experimental research (Bakker and Sevenster, 1995). As in his mouse project, Theo established breeding lines, selecting for differences in aggressiveness (Bakker, 1986). For his thesis, entitled 'Aggressiveness in sticklebacks (*Gasterosteus aculeatus* L.): a behaviour-genetic study', he examined individual aggressiveness in different developmental stages and contexts and their intercorrelations. It was eventually published as a 144-page (!) paper in the journal *Behaviour* (Bakker, 1986) and can be considered pioneering work in recent animal personality research. It was highly fitting that in 1990 Theo won the Niko Tinbergen Prize, awarded by the German Ethological Society, for his PhD thesis.

After finishing his PhD studies, Theo remained as postdoctoral researcher in Sevenster's group for two more years, continuing his work on the genetical background of aggression in stickleback (Bakker and Sevenster, 1989; Bakker *et al.*, 1989). At that time, he regularly received invitations from abroad for working visits, for example to Felicity Huntingford (University

Fig. 1. A courting male threespine stickleback at his nest. Males develop the bright red throat and blue eye coloration only during the mating season, making them highly attractive for receptive females. Credit: Photo by Joachim Frommen and Fabian Herder.

of Glasgow) in the United Kingdom and to Frederick Whoriskey (McGill University) and Gerard FitzGerald (Université Laval) in Canada. One of these visits brought him into contact with Manfred Milinski, who offered him a position as *wissenschaftlicher Assistent* (comparable to an assistant professor) at the Ethological Station Hasli of the University of Bern, Switzerland. Theo and his family moved to Bern in 1988.

In Bern, Theo and Manfred Milinski were among the first to experimentally test the theoretical explanations for the evolution of female mate preference (reviewed in Bakker, 1990). As predicted by Zahavi (1975) and Hamilton and Zuk (1982), they showed that the intensity of a stickleback male's red coloration reflects his physical condition and parasite load. Because females prefer more intensely red-coloured males, they avoid parasitized males (Milinski and Bakker, 1990). This fundamental paper has been widely cited (almost 800 citations up until 2018) and cemented the importance of the threespine stickleback as a model system in sexual selection research. Next, Theo demonstrated a genetic correlation between male ornament expression and female preference (Bakker, 1993), providing unique empirical evidence for Fisher's 'runaway process' (Fisher, 1930). The following report of variation in female mate choice (Bakker *et al.*, 1999) represented a further breakthrough for the study of sexual selection, suggesting that not only the expression of male ornaments but also female preference is condition-dependent. These three studies were published in *Nature* and became textbook examples of sexual selection (e.g. Davies *et al.*, 2012). During that time, Theo further continued visiting labs abroad. One of those was a stay at Indiana University, USA with William 'Bill' Rowland. This trip was not only scientifically stimulating (Bakker and Rowland, 1995; Bakker, 2010), but also memorable because of musical evenings during which Theo played the triangle.

In 1994, Theo finished his *habilitation* treatise entitled 'The evolution of male ornamentation through female choice in three-spined sticklebacks, *Gasterosteus aculeatus* L.', which included the above-mentioned ground-breaking papers on sexual selection among others. Accordingly, he received the *venia docendi* in Zoology from the University of Bern, which accompanied his promotion to the rank of associate professor. Theo and his group, which consisted of several PhD students and postdocs, pursued research on sexual selection (e.g. Bakker and Mundwiler, 1994; Kraak and Bakker, 1998; Kraak *et al.*, 1999, 2000; Künzler and Bakker, 2000; Mazzi *et al.*, 2002, 2003). Inspired by the classical stickleback dummies that had been used since Tinbergen's early studies (Ter Pelwijk and Tinbergen, 1937; Rowland, 1982), Theo and his team became interested in developing highly standardized artificial stimuli for experiments in sexual selection. Here, they took advantage of the rapidly developing computer technology that allowed them to create computer-animated stickleback (Künzler and Bakker, 1998). They were therefore among the pioneers in using computer animations, a technique that is today used widely in behavioural research (Baldauf *et al.*, 2008; Chouinard-Thuly *et al.*, 2017). These virtual stickleback males found various applications, including in mate-choice (e.g. Künzler and Bakker, 2001; Mazzi *et al.*, 2004) and sperm competition experiments (e.g. Zbinden *et al.*, 2003). Additionally, Theo started working on host–parasite relationships in Bern. He focused especially on acanthocephalan fish and bird parasites with complex life cycles, changing the behaviour and colour of their intermediate host, i.e. gammarid amphipods (Bakker *et al.*, 1997; Mazzi and Bakker, 2003).

In 1999, Theo accepted a chair in Animal Ecology (succeeding Gerhard Kneitz) at the Institute for Evolutionary Biology and Ecology of the Rheinische-Friedrich-Wilhelms-University of Bonn in Germany headed at the time by Klaus Peter Sauer. In Bonn, Theo further expanded his research interests, encouraging his students to work on a broad variety of topics in behavioural and evolutionary ecology. The aim of a first new project was to elucidate functions and mechanisms of kin discrimination in stickleback. It revealed that

stickleback possess the ability to differentiate siblings from unrelated individuals and that they use this ability in all crucial behavioural decisions, including shoaling (e.g. Frommen and Bakker, 2004; Frommen *et al.*, 2007a, 2007b), mate choice (Frommen and Bakker, 2006; Mehlis *et al.*, 2008), and brood care (Mehlis *et al.*, 2010). His interest in the effects of relatedness on mate choice eventually led Theo to integrate a new model species into his research. The biparental African cichlid fish, *Pelvicachromis taeniatus*, shows ornaments in both sexes and mutual mate choice (Thünken *et al.*, 2007a; Baldauf *et al.*, 2009). In contrast to most other animal species, this fish does not avoid inbreeding, but represents a rare example of kin mating preference (Thünken *et al.*, 2007a; Langen *et al.*, 2011; Thünken *et al.*, 2012). Examination of the underlying proximate kin recognition mechanism in this cichlid was a consequent research focus (Hesse *et al.*, 2012; Thünken *et al.*, 2014). Moreover, *P. taeniatus* proved to be an ideal model system to investigate the function of sexual ornaments in females (e.g. Baldauf *et al.*, 2010, 2011) or the importance of the social environment on social and mating behaviour (Hesse *et al.*, 2016), and to study the causes and consequences of predator-induced phenotypic plasticity (e.g. Meuthen *et al.*, 2016, 2018a). The extraordinarily long sperm of *P. taeniatus* was another unexpected finding (Thünken *et al.*, 2007b; Langen *et al.*, 2017).

Besides these new research avenues, Theo and his team continued to investigate the importance of visual cues in stickleback behaviour. They elucidated the role of ultraviolet-A (UVA) light in sexual signalling (Rick *et al.*, 2004, 2006; Rick and Bakker, 2008a, 2008b, 2008c; Hiermes *et al.*, 2015a), shoaling behaviour (Modarressie *et al.*, 2006, 2015; Hiermes *et al.*, 2015b), visual foraging (Rick *et al.*, 2012), and predation risk (Modarressie *et al.*, 2013). Recent projects focused on the ecological costs of increased levels of ambient ultraviolet-B (UVB) radiation (Vitt *et al.*, 2017a, 2017b). A related PhD project addressed the co-evolution between stickleback and their parasites in the lakes of the Outer Hebrides, Scotland (e.g. Rahn *et al.*, 2016a, 2016b). Furthermore, the aforementioned study on genetic co-variation between female preference and male red coloration in stickleback (Bakker, 1993) was extended in Bonn by including the role of visual physiology (Rick *et al.*, 2011).

Because sexual selection does not stop after mating but continues at the gamete level (Parker, 1970) and because sneaking and multiple paternity are widespread in natural stickleback populations (Largiadèr *et al.*, 2001), it was perhaps logical that Theo had already begun to include sperm competition as part of his research agenda when in Bern (e.g. Zbinden *et al.*, 2001, 2004). This project was successfully extended in Bonn by studying the environmental and genetic contributions to variation in sperm and testes traits, including food restriction and carotenoid supplementation (Mehlis *et al.*, 2015a), temperature (Mehlis and Bakker, 2014), and inbreeding (Mehlis *et al.*, 2012). Another aim was to investigate the mechanisms of post-copulatory intra- and intersexual selection in stickleback at the level of fertilization (e.g. Bakker *et al.*, 2006, 2014; Mehlis *et al.*, 2015a, 2015b). Further research objectives were sex reversal (Bakker, 2016) and molecular-genetic approaches for sex determination (Bakker *et al.*, 2017b) or paternity analyses (Langen *et al.*, 2013). Finally, Theo continued his work on freshwater amphipods that serve as intermediate host for different acanthocephalan parasites (Bakker *et al.*, 2017a). In particular, various studies examined the anti-predator behaviour of *G. pulex* and its manipulation by parasites (e.g. Baldauf *et al.*, 2007; Kullmann *et al.*, 2008; Thünken *et al.*, 2010).

During his career, Theo supervised 15 PhD students and more than 50 graduate and countless undergraduate projects. Most of them were funded by the Swiss National Science Foundation (SNSF) and the German Research Foundation (DFG). Besides his passion for research, Theo was a popular teacher. In practical courses for undergraduate and graduate students on 'Behavioral Ecology', Theo conveyed the importance of well-planned

experimental approaches, including innovative methods as well as exciting experiments based on current research papers. These courses enabled students to gain deep insights into scientific research early in their careers. Theo further gave lectures and offered seminars covering a variety of subjects ranging from the basics in ecology to more advanced topics in behavioural ecology. Besides teaching Theo was always strongly involved in academic administration. For many years, he was the head of the examination committee of the international master program in Organismic Biology, Evolutionary Biology and Palaeobiology (OEP-Biology) that provides students with a fundamental understanding of evolutionary research, linking its various sub-disciplines. Theo was highly integrated within the international scientific community and joined the editorial boards of leading journals in his field, including *Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, and the *Journal of Evolutionary Biology*. Since 2011 he has served together with James Traniello as Editor in Chief of *Behavioral Ecology and Sociobiology* (Bakker and Traniello, 2011). Together they positioned the journal strongly against plagiarism and intellectual theft (Traniello and Bakker, 2016) and advocated science as the central source of truth (Traniello and Bakker, 2017).

His team recognized Theo Bakker not only as an enthusiastic, highly motivating, creative and supportive researcher and teacher, but also as a very cheerful person with a very distinctive sense of humour. We will never forget his lecture on the morning of *Weiberfastnacht* (that is, the Thursday that the street carnival in Bonn starts), when he suddenly disappeared behind his desk to reappear with a screaming green wig on his head, and nonchalantly continued giving the lecture. Moreover, the tradition of rowing freshly promoted PhD students over the institute's pond in a way-too-small rubber boat will remain legendary. With his optimistic attitude, Theo always encouraged students to write up their results or re-submit rejected manuscripts; he patiently corrected hundreds of manuscript drafts in his constructive manner. He was always a fair and generous group leader, encouraging his team members to follow their personal research interests and to develop their own profile. At the same time, his office door was always open to discuss scientific or personal topics. Upon his retirement, Theo has not thought about quitting science. Luckily, there are still many data to analyse and papers to write, true to the motto 'testing, not guessing'.

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